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Mustura arenaria, a new species of genus *Mustura* (Cypriniformes, Nemacheilidae) from Myanmar, with taxonomic notes on *Mustura shanensis*

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Abstract

Mustura arenaria **sp. nov.**, a new species of the genus *Mustura*, is described from the Chindwin–Irrawaddy basin in central Myanmar. It can be distinguished from other congeners by the following combination of characters: 7–15 vertical lateral blotches alternating with 9–17 saddles, distinctly narrower than the interspaces; lateral blotches more rounded in males; 8+8 branched caudal-fin rays; 8½ branched dorsal-fin rays; and a complete lateral line. Phylogenetic analysis based on combined data of Cyt *b* and RAG1 revealed that the new species represents an independent lineage and that *Mustura* is paraphyletic. Additionally, both morphological and molecular data support the transfer of *Mustura shanensis* to the genus *Schistura*. Notably, a comprehensive taxonomic revision of this genus and related taxa involving more species is required because the genetic positions of several *Mustura* species conflict with morphological characters.

Key Words

Chindwin–Irrawaddy basin, loach, phylogeny, species description, taxonomy

Introduction

The loach genus *Mustura* was established by Kottelat (2018), designating *Mustura celata* Kottelat, 2018, as the type species. The genus is characterized by the following characters: a small free posterior chamber present or absent; two air-bladder capsules connected by a manubrium; the pectoral fin slanted upwards and expanded laterally in males, with the first branched ray being the widest, its branches close together and without a membrane except near the tip; the lower lip with a wide median incision, its two halves forming an acute angle; and the suborbital flap with small tubercles on the posterior extremity (Kottelat 2018).

In the revision of the genus *Physoschistura* Bănărescu & Nalbant, 1982, and related taxa, Kottelat (2018) transferred *P. chindwinensis* Lokeshwor & Vishwanath, 2012, *P. chhimtuipuiensis* Lalramliana, Lalhlimpuia,

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Solo & Vanramliana, 2016, *P. prashadi* (Hora, 1921), *P. yunnaniloides* Chen, Kottelat & Neely, 2011, *P. tigrina* Lokeshwor & Vishwanath, 2012, *P. tuivaiensis* Lokeshwor, Vishwanath & Shanta, 2012, *P. harkishorei* Das & Darshan, 2017, and *Schistura shuensis* Bohlen & Šlechtová, 2014 to *Mustura*. He tentatively classified *P. shanensis* (Hora, 1929), *P. dikrongensis* Lokeshwor & Vishwanath, 2012, *P. walongensis* Tamang & Sinha, 2016, *S. bella* Kottelat, 1990, and *S. maepaiensis* Kottelat, 1990 as *Mustura*, noting that while the majority of diagnostic characters align with the genus, several morphological characters deviate from typical *Mustura* species. Additionally, he pointed out that the taxonomic status of *P. chulabhornae* Suvarnaraksha, 2013, *P. shuangjiangensis* (Zhu & Wang, 1985), *S. geisleri* Kottelat, 1990, and *S. isostigma* Kottelat, 1998, remained uncertain, suggesting that they might be provisionally placed in *Mustura* (Kottelat 2018). Subsequently, four additional species, namely *M. subhashi* Choudhury, Das, Bharali, Sarma, Tyagi, Lal & Sarma, 2021, *M. taretensis* Chinglemba, Rameshori & Vishwanath, 2021, *M. daral* Rameshori, Chinglemba, Darshan & Vishwanath, 2022, and *M. yangi* Qin, Kottelat, Kyaw & Chen, 2022, were described, and morphological evidence supported the taxonomic status of *M. dikrongensis* (Chinglemba et al. 2021; Choudhury et al. 2021; Qin et al. 2022; Rameshori et al. 2022). Therefore, there are currently 22 valid species in the genus *Mustura* sensu lato distributed throughout South and Southeast Asia. However, *M. shanensis*, *M. bella*, *M. shuangjiangensis*, *M. geisleri*, and *M. isostigma* might not belong to *Mustura*, according to limited molecular phylogenetic data that contradict morphological interpretations (Dvořák et al. 2023; Šlechtová et al. 2025). *Mustura shuangjiangensis* was classified into the new genus *Zhutura* in a recent study (Endruweit 2025).

From 2016 to 2024, systematic surveys were conducted in the Chindwin–Irrawaddy River basin in Myanmar, resulting in a number of loach specimen collections. These specimens include a previously undescribed species, as indicated by thorough morphological and phylogenetic analyses. Therefore, we formally describe this new species herein.

Materials and methods

Morphological analysis

Specimens used for morphological studies were fixed and preserved in 10% formalin. Tissue samples were cryopreserved at −80 °C after being kept in absolute ethanol. Counts and measurements were taken on the fish specimens' left side following Kottelat (1990). Measurements were taken point-to-point using dial calipers, with values recorded to the nearest 0.1 mm. Vertebrae counts were taken from X-ray photographs. Comparative data for other *Mustura* species were derived from original descriptions and associated publications (Kottelat 1990, 2018; Chen et al. 2011; Lokeshwor and Vishwanath 2012b, 2012a, 2012c; Lokeshwor et al. 2012; Bohlen and Šlechtová 2014; Lalramliana et al. 2016; Tamang and Sinha 2016; Das and Darshan 2017; Chinglemba et al. 2021; Choudhury et al. 2021; Qin et al. 2022; Rameshori et al. 2022).

Abbreviations: ex., examined specimens; SL, standard length; SD, standard deviation; n, number; KIZ, Kunming Institute of Zoology, Kunming; SEABRI, Southeast Asia Biodiversity Research Institute, Nay Pyi Taw.

DNA extraction, PCR, and sequencing

Genomic DNA was extracted from fin tissues using the FastPure Cell/Tissue DNA Isolation Mini Kit (Vazyme Biotech). Two genes were used for amplification and sequencing: the mitochondrial cytochrome b (Cyt *b*) using primers L14724 and H15915, and the nuclear recombination-activating gene 1 (RAG1) using primers RAG1-F and RAG-RV1 (Xiao et al. 2001; Perdices et al. 2005; Šlechtová et al. 2007). PCR amplifications were performed in a 30 μL reaction volume comprising 15 μL San mix Taq, 2 μL of each primer, 2 μL of template DNA, and 9 μL ddH_2O. The thermocycling conditions were as follows: pre-denaturation at 94 °C for 4 min; 35 cycles of denaturation at 94 °C for 30 s, annealing at 53 °C (for RAG1) or 54 °C (for Cyt *b*) for 45 s, extension at 72 °C for 90 s; and a final extension at 72 °C for 10 min. Sequencing was performed by Sangon Biotech.

Phylogenetic analysis

The phylogenetic analysis included 57 Cyt *b* and 54 RAG1 sequences in total (Suppl. material 1: table S1). Three species from different genera were selected as outgroups following the results of Šlechtová et al. (2025).

Sequences were assembled using the SeqMan module of DNAStar (Burland 1999). Phylogenetic analyses were performed using PhyloSuite 1.2.3 (Xiang et al. 2023). Sequences were aligned using MAFFT 7 with default parameters and trimmed using Gblocks (Castresana 2000; Katoh and Standley 2013). The incongruence length difference test (ILD) was assessed using PAUP.4 (Swofford 2003). The best-fitting nucleotide substitution models were selected using ModelFinder (for single genes) and PartitionFinder 2 (for combined gene data) under the Akaike information criterion corrected (AICc) (Suppl. material 1: table S2) (Lanfear et al. 2016; Kalyaanamoorthy et al. 2017).

Phylogenetic trees were constructed using IQ-TREE 2.1.3 for maximum likelihood (ML) and MrBayes 3.2.7 for Bayesian inference (BI) (Ronquist et al. 2012; Minh et al. 2020). The ML analysis was run with 10,000 ultrafast bootstrap replicates and 1,000 Shimodaira–Hasegawa likelihood ratio tests (SH-aLRT) until a correlation coefficient of ≥ 0.99 was reached (Hoang et al. 2018). The BI analysis was conducted independently using four Markov chain Monte Carlo (MCMC) chains (three hot and one cold) initiated from a random tree. Each chain was run for 10 million generations and sampled every 1,000 generations,

with the first 25% of samples discarded as burn-in. Runs were considered convergent when the standard deviation of split frequencies was less than 0.01. Resulting phylogenetic trees were visualized and edited using iTOL (Letunic and Bork 2024). Based on the Cyt *b* gene, pairwise uncorrected genetic distances were calculated with 1,000 bootstrap replicates using the Kimura two-parameter (K2P) model in MEGA 11 (Tamura et al. 2021).

Result

Mustura arenaria Lyu, Lin & Chen, sp. nov.

https://zoobank.org/59B59DCD-3A5E-4B7E-A67D-58BAC24219EA

Holotype. SEABRI 20164206, male, 29.3 mm SL, Yaw Stream, a tributary of Yebya River at Pakokku City, Magway Region, Myanmar, 21°26'24.86"N, 94°31'5.21"E, 142 m asl., Xiao-Yong Chen, Tao Qin, Shu-Sen Shu, Khin Mar Mint & Thinn Su Tin, 22 Dec. 2016.

Paratypes. SEABRI 20164207, 1 ex., 25.8 mm SL, same as holotype. SEABRI 20170634–38, 42–44, 48, 50, 52, 56, 12 ex., 27.7–39.5 mm SL, Myan Aww Stream, a tributary of the Chindwin River at Larboh village, Alaungdaw Kathapa National Park, Sagaing Region, Myanmar, 22°34'53.46"N, 94°30'51.84"E, 169 m asl., Xiao-Yong Chen, Tao Qin, Shu-Sen Shu, Paing Zaw & Ye Yint Tun, 21 June 2017; SEABRI 20170752–53, 2 ex., 34.4–36.8 mm SL, Salin Stream at Nwetamal Village, Sinbyugyun Town, Salin Township, Magway Region, Myanmar, 20°39'44.58"N, 94°41'13.98"E, 58 m asl., Xiao-Yong Chen, Tao Qin, Shu-Sen Shu, Paing Zaw & Ye Yint Tun, 24 June 2017; SEABRI 20170522, 1 ex., 30.3 mm SL, Lower Yemar River, about 10 km upstream of Monywa, Sagaing Region, Myanmar, 22°8'59.64"N, 95°3'26.10"E, 76 m asl., Xiao-Yong Chen, Tao Qin, Shu-Sen Shu, Paing Zaw & Ye Yint Tun, 19 June 2017; KIZ-PZ20180138, 1 ex., 31.2 mm SL, Nam Sa Pi Stream at Htamanthi, Sagaing Region, Myanmar, 25°21'33.84"N, 95°20'43.32"E, 127 m asl., Paing Zaw & Nay Htet Naing, 8 May 2018; SEABRI 20192385, 1 ex., 29.9 mm SL, Lae Pon Stream, Indawgyi Lake, Kachin State, Myanmar, 25°2'55.72"N, 96°21'1.70"E, Thinn Su Tin & Lamin Ko Ko, 12 May 2019.

Non-types. SEABRI 20170639–41, 45–47, 49, 51, 53–55, 57–63, 18 ex., 28.4–33.4 mm SL, Myan Aww Stream, a tributary of Chindwin River at Larboh village, Alaungdaw Kathapa National Park, Sagaing Region, Myanmar, 22°34'53.46"N, 94°30'51.84"E, 169 m asl., Xiao-Yong Chen, Tao Qin, Shu-Sen Shu, Paing Zaw & Ye Yint Tun, 21 June 2017.

Diagnosis. *Mustura arenaria* is distinguished from its congeners by the following combination of characters: 7–15 lateral blotches alternating with 9–17 saddles, distinctly narrower than interspaces; blotches more elongated in females and more rounded in males; two dark stripes extending from snout tip to the anterior dorsum of eye, forming an "X" pattern, but not fused; a pair of blotches surrounding the fontanel, extending from posterior dorsal of eye to nape, and forming a triangle marking; 8½ branched dorsal-fin rays; 8+8 branched caudal-fin rays; lateral line complete; axillary pelvic lobe present; upper lip with a small notch.

Description. See Fig. 1 for general appearance and Table 1 for morphometric data. Body moderately elongated, deepest body depth slightly anterior to dorsal-fin origin, with depth gradually decreasing from dorsal-fin origin to caudal-fin base. Body rounded to slightly compressed anteriorly, compressed posteriorly. Head depressed, dorsal profile arched, decreasing markedly anterior to eye. Snout slightly pointed. Interorbital area wide and flat. Eye oval, near top of head, not visible in ventral view. Cheeks not swollen. Caudal peduncle 1.0–1.7 times longer than deep. Low dorsal and ventral keels present posteriorly on caudal peduncle. Largest recorded size 39.5 mm SL.

Dorsal-fin rays iii-8$^{1}/_{2}$, distal margin truncated, extending beyond vertical through anus but not reaching anal-fin origin. Pectoral-fin rays i-9–10, slightly falcate, reaching beyond two-thirds of distance between origin pectoral and pelvic fins, second branched ray longest. Pelvic-fin rays i-6, reaching close to or through anus, origin opposite of the first or second branched dorsal-fin ray. Axillary pelvic lobe present. Anus situated about twice eye diameters in front of anal-fin origin. Anal-fin rays ii-5$^{1}/_{2}$, distal margin truncated, origin closer to caudal-fin base than pelvic-fin origin. Caudal-fin rays 8+8, forked, lower lobe slightly longer than upper, longest ray 1.3–1.7 times length of median rays.

Table 1. Morphometric data of *Mustura arenaria* (n = 17). Range, mean, and SD include holotype data.

	Holotype	Rang	Mean ± SD
Standard length (mm)	29.3	25.8–39.5	–
Total length (mm)	36.5	32.2–49.6	–
% of standard length			
Total length	124.6	119.1–131.8	126.0 ± 2.7
Head length (dorsal)	18.8	15.6–21.1	18.5 ± 1.2
Head length (lateral)	23.9	21.8–24.8	22.9 ± 0.8
Predorsal length	50.9	46.2–51.7	49.2 ± 1.5
Prepelvic length	51.5	48.2–53.4	51.1 ± 1.2
Preanus length	63.1	63.1–72.4	68.8 ± 2.1
Preanal length	75.8	73.8–81.1	77.1 ± 1.9
Head depth	11.9	11.9–14.9	13.6 ± 0.8
Body depth at dorsal-fin origin	16.7	15.9–20.5	18.1 ± 1.5
Depth of caudal peduncle	10.3	8.7–10.5	9.6 ± 0.5
Length of caudal peduncle	14.3	10.4–15.5	13.4 ± 1.6
Head width	13.3	13.3–17.5	15.7 ± 1.2
Body width at dorsal-fin origin	13.7	11.0–17.1	13.7 ± 1.4
Snout length	7.8	6.1–7.9	7.1 ± 0.6
Eye diameter	5.1	4.6–5.9	5.2 ± 0.4
Interorbital width	5.8	5.2–7.5	6.3 ± 0.6
Dorsal-fin length	18.1	18.1–22.0	20.6 ± 1.1
Pectoral-fin length	22.5	21.1–24.8	23.1 ± 1.1
Pelvic-fin length	15.0	15.0–18.1	16.8 ± 0.8
Anal-fin length	16.7	13.5–19.1	16.7 ± 1.3
% of dorsal head length			
Snout length	41.8	32.8–43.9	38.3 ± 3.2
Eye diameter	27.3	24.3–32.2	28.1 ± 2.2
Interorbital width	30.9	27.7–40.6	34.2 ± 3.2
% of lateral head length			
Snout length	32.9	26.8–33.3	30.8 ± 2.0
Eye diameter	21.4	19.5–26.0	22.7 ± 1.9
Interorbital width	24.3	23.1–32.6	27.5 ± 2.4

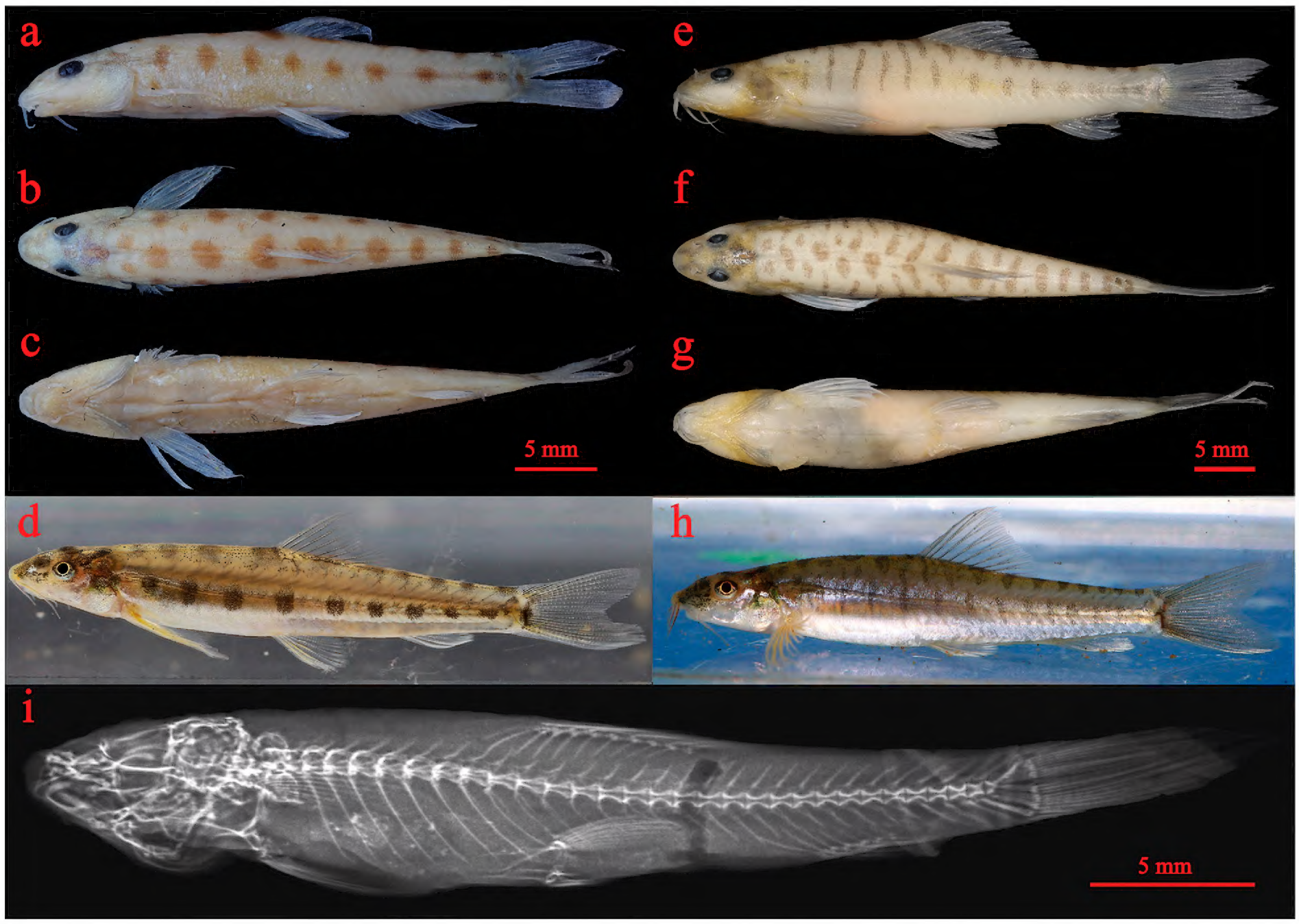

Figure 1. *Mustura arenaria*. **a–d.** Lateral, dorsal, and ventral views and a living photo of male, holotype SEABRI 20164206, 29.3 mm SL; **e–h.** Lateral, dorsal, and ventral views and a living photo of female, paratype SEABRI 20170634, 39.0 mm SL (h is 180° inverted); **i.** X-ray of paratype SEABRI 20192385, 29.9 mm SL.

Body entirely covered by scales, absent between base of pectoral fins and belly in front of pelvic-fin. Lateral line complete. Cephalic lateral line system with 6–9 supraorbital, 3+8–13 infraorbital, 6 preoperculo-mandibular, and 3 supratemporal pores. Tubercles present on barbels, dorsal head, and dorsal side of branched pectoral-fin rays.

Mouth inferior, small, strongly arched, gape about twice as wide as long (Fig. 2a). Nostrils adjacent, anterior one on front side of a flap-like tube, not reaching eye. Lips thick and deeply furrowed; upper lip slightly notched medially; lower lip deeply interrupted medially, forming two triangular pads. *Processus dentiformis* week. Lower jaw without median notch. Three pairs of elongate barbels. Inner rostral barbel reaching close to or through anterior margin of eye; outer one reaching close to or surpassing posterior margin of eye. Maxillary barbel reaching through posterior margin of eye. Two halves of air bladder capsule connected by a manubrium; posterior chamber free, small, unossified (Fig. 2c). Intestine with a small bend (Fig. 2e). Vertebral count 4+28–29 (n = 2) (Fig. 1i).

Coloration. In life: Body translucent. Dorsal and lateral sides of body light brown, ventral silvery. Saddles and blotches dark brown. Dorsal and lateral head with black blotches. Snout tip light brown, dark around nostrils. Barbels brownish. All fin membranes hyaline. Dorsal-fin and caudal-fin rays gray.

Preserved in 10% formalin. Head and body pale whitish to yellowish. Body with 7–15 vertically elongated lateral blotches, narrower than interspaces, anterior more elongated, alternating with 9–17 saddles. Lateral blotches more rounded in males. Basal caudal bar dissociated and faint, forming an upper small spot (usually absent) and a lower elongated blotch. Two dark stripes extending from snout tip to dorsum of anterior nostrils, not connected; a pair of small faint blotches between dorsal nostrils, forming an "X"-shaped pattern together with stripes. A pair of elongated blotches in interorbital space. A pair of blotches surrounding fontanel from posterior dorsal eye to nape, forming a triangle mark (Fig. 2b). Ventral side of head yellow, more intense on gill arches. Dorsal-fin membranes hyaline, with 1–2 rows of faint spots on branched rays. Pectoral, pelvic, and anal-fin rays hyaline. Caudal fin hyaline to grayish. Barbels white, bearing a few scattered melanophores dorsally.

Sexual dimorphism. Males with a longer and stretched downward suborbital flap with small tubercles (Fig. 3c); females with either a small suborbital flap, groove, or lacking it (Fig. 3a, b). In males, first branched pectoral-fin ray wider and slightly upward, without membrane between branches except near tip (Fig. 2d). Lateral blotches more elongated in females (Fig. 1e–h), and more rounded in males (Fig. 1a–d). Tubercles on snout, dorsal and lateral sides of head more developed in males.

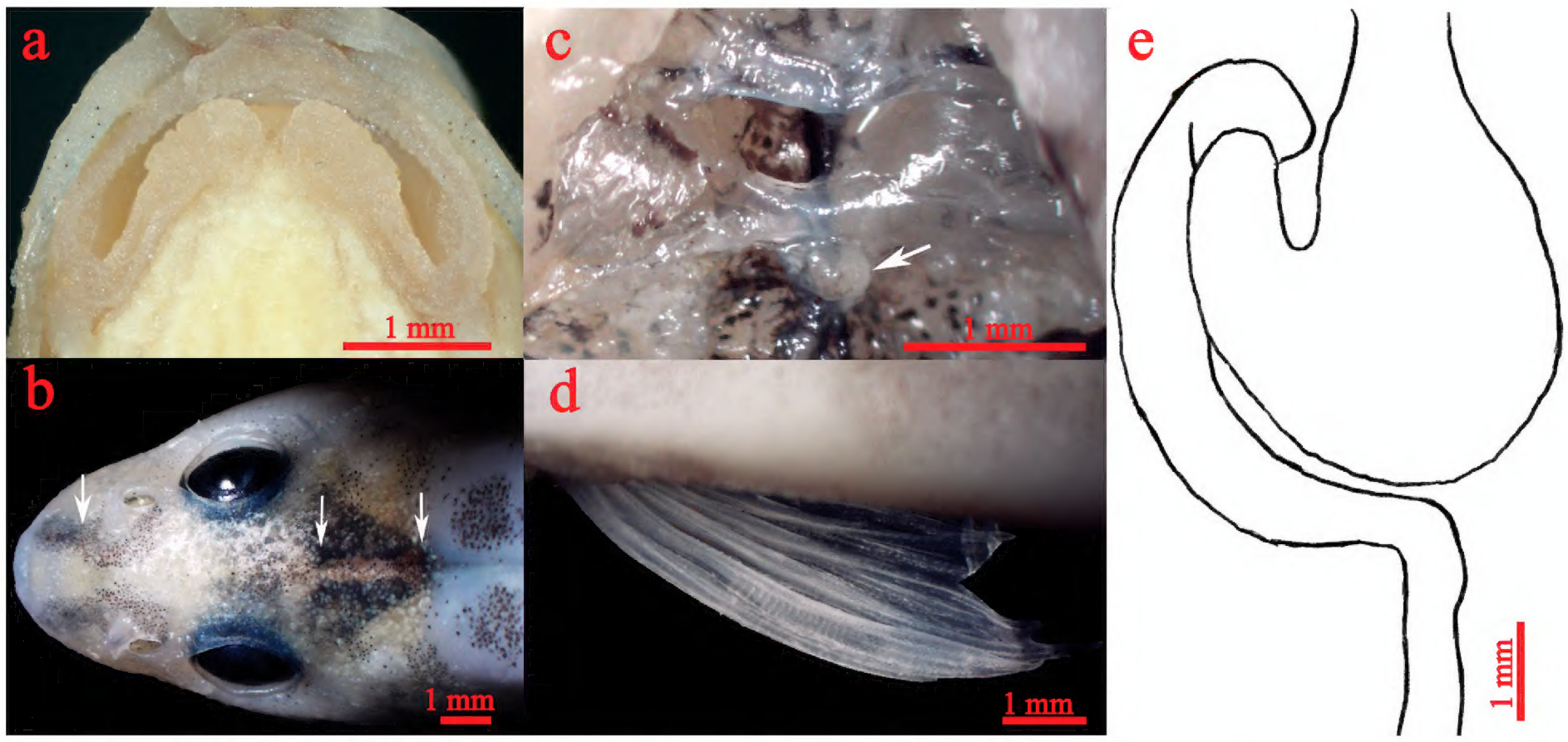

Figure 2. *Mustura arenaria*. **a, c, e.** Lip structure, air bladder, and intestine of SEABRI 20170635, 39.5 mm SL; **b.** Dorsal view of head of SEABRI 20170634, 39.0 mm SL; **d.** Expanded first branched pectoral-fin ray in male, SEABRI 20170753, 34.4 mm SL.

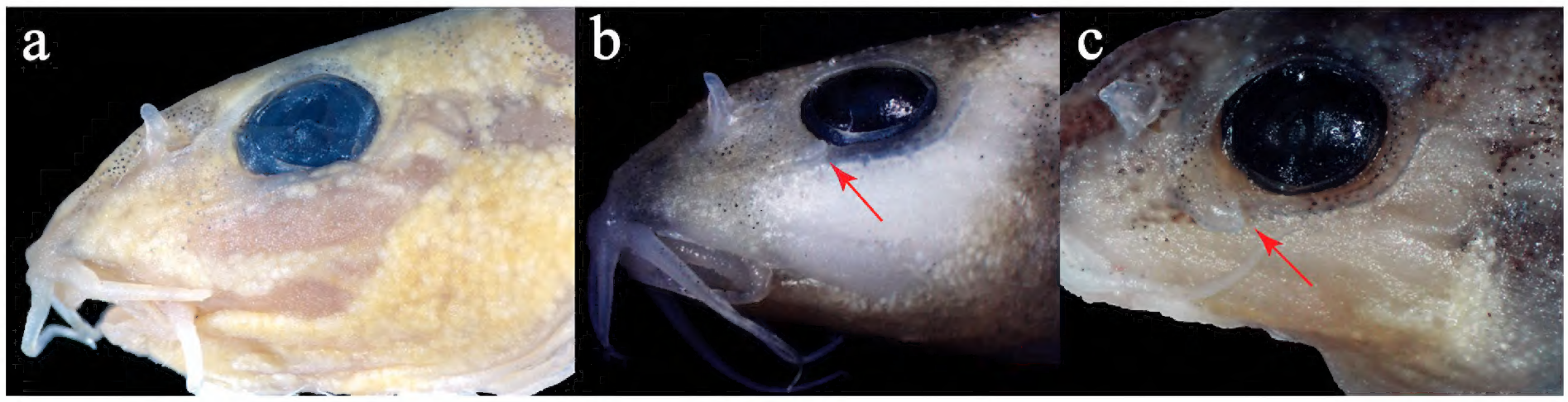

Figure 3. Suborbital area of *Mustura arenaria*. **a.** SEABRI 20170522, female, 30.3 mm SL (lacking suborbital flap); **b.** SEABRI 20170634, female, 39.0 mm SL (small suborbital flap); **c.** SEABRI 20170649, male, 35.6 mm SL (suborbital flap).

Etymology. The specific epithet "*arenaria*" is derived from the Latin word "arena" (meaning "sand"), feminine in gender, in reference to the species' preference for sandy substrate habitats. The Chinese name is suggested as 沙迷鰍.

Habitat. *Mustura arenaria* was observed in the Chindwin-Irrawaddy River drainage. It prefers flowing water in streams with fine sandy substrates and occurs in small aggregations (Fig. 4). Sympatric species recorded at type localities include: *Anguilla bengalensis* (Gray, 1831), *Pangio signicauda* Britz & Maclaine, 2007, *Schistura callidora* Bohlen & Šlechtová, 2011, *Opsarius barnoides* (Vinciguerra, 1890), *Hypsibarbus oatesii* (Boulenger, 1893), *Pethia stoliczkana* (Day, 1871), *Glyptothorax ngapang* Vishwanath & Linthoingambi, 2007, *G. trilineatus* Blyth, 1860, and *G. burmanicus* Prashad & Mukerji, 1929.

Distribution. *Mustura arenaria* is currently known from the Chindwin-Irrawaddy River drainage, including Indawgyi Lake (Fig. 5). It is expected to spread more widely throughout tributaries of the Irrawaddy basin in central Myanmar, particularly in the dry zone of the Sagaing, Mandalay, and Magway regions.

Figure 4. Habitat of *Mustura arenaria*. Myanmar: Sagaing Region: Alaungdaw Kathapa National Park: Larboh Village: Myan Aww Stream, a tributary of the Chindwin River.

Phylogenetic analysis. The ILD test revealed no significant conflict between the Cyt *b* and RAG1 genes ($p = 0.335$). The genus *Mustura* was recovered as

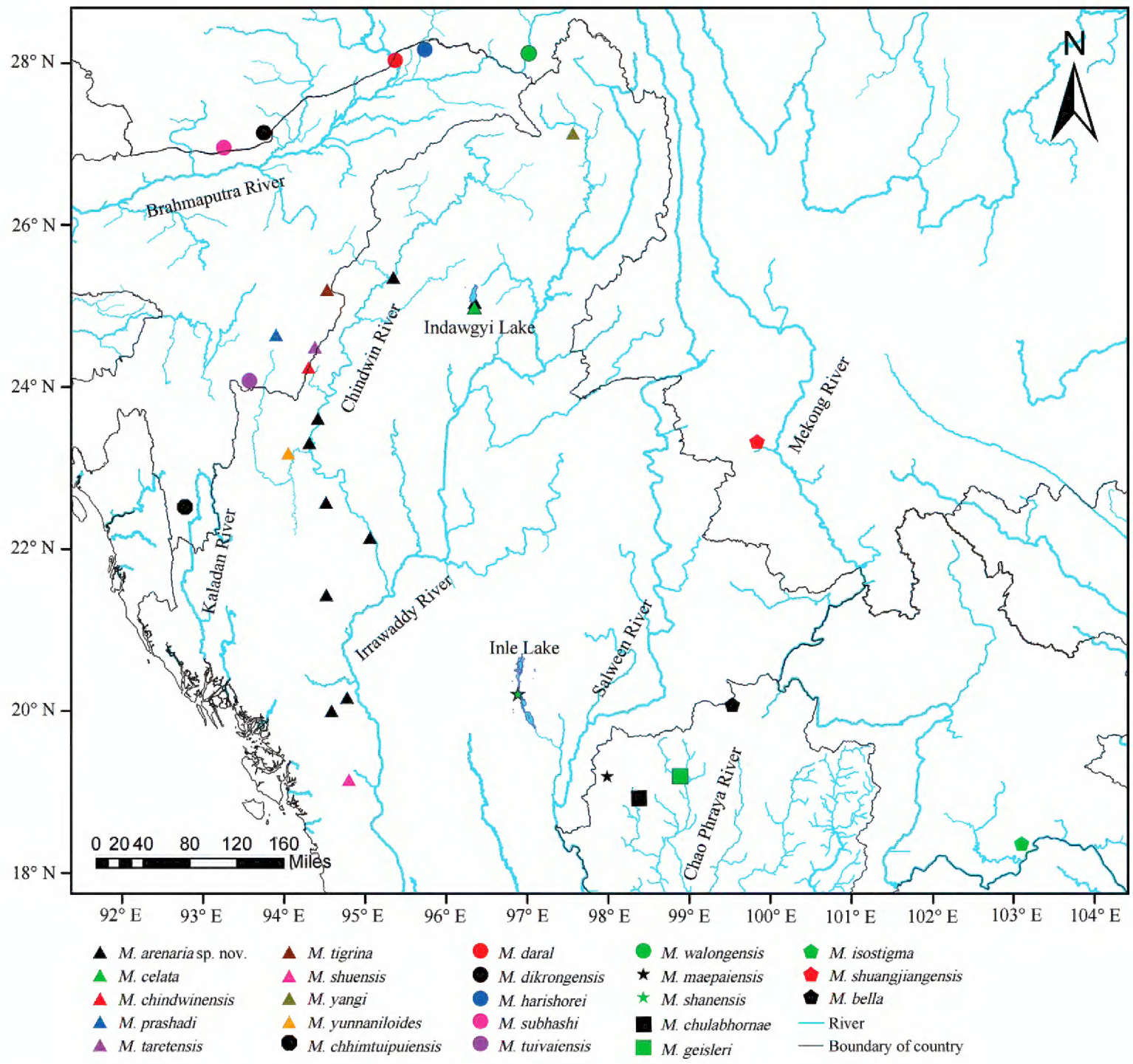

Figure 5. Map showing type localities of species of *Mustura*.

polyphyletic in the phylogenetic analyses constructed from Cyt *b*, RAG1, and combined datasets, respectively. These results also strongly supported the distinct species status and monophyly of the new species, *M. arenaria* sp. nov. However, a single gene contains only a limited amount of phylogenetic information. The topological structures of the two single-gene trees differed markedly from those of previous studies and were weakly supported (Suppl. material 1: figs S1, S2). Conversely, the phylogenetic analysis based on the combined dataset was consistent with previous findings (Fig. 6). Consequently, the discussion herein is based on the analysis of the combined data.

The K2P genetic distance based on Cyt *b* between *M. arenaria* and its congeners ranged from 13.49% to 16.16%. The minimum K2P distance (9.46%) was observed between *Mustura* sp. UF192977 and *M. yangi*, whereas the maximum distance (18.57%) was found between *Mustura* sp. Magway and *M. geisleri*. The intraspecific genetic distance within *M.* arenaria was 1.19% (Table 2).

Comparisons

Species of *Mustura* can be divided into two groups based on whether the lateral line is complete or incomplete. *Mustura arenaria*, together with *M. bella*, *M. celata*, *M. chindwinensis*, *M. daral*, *M. harkishorei*, *M. maepaiensis*, *M. prashadi*, *M. shanensis*, *M. shuensis*, *M. subhashi*, *M. taretensis*, *M. tigrina*, *M. tuivaiensis*, *M. yangi*, *M. yunnaniloides*, *M. isostigma*, and *M. shuangjiangensis*, belongs to the complete lateral-line group. A detailed comparison of diagnostic characters among *Mustura* species is provided in Table 3.

Within the complete lateral-line group, *M. arenaria* can be readily distinguished from species with continuous lateral bars by having 7–15 lateral blotches alternating with 9–17 dorsal saddles. The lateral color patterns of these species are as follows: 12–30 bars, occasionally separated by a distinctly yellow stripe, and a stripe along the lateral line in *M. bella*; 9–10 bars in *M. daral*; 10–13 bars in *M. maepaiensis*; 7–10 bars in *M. shanensis*; 6–9 bars with a faint stripe in *M. shuensis*; 14–23 bars in *M. subhashi*; and 10–21 bars in *M. shuangjiangensis*. *Mustura arenaria* differs from *M. bella*, *M. daral*, *M. maepaiensis*, *M. shuensis*, and *M. subhashi* by having 8+8 (vs. 9+8) caudal-fin rays, a caudal fin without pigment (vs. with V-shaped markings), $8^1/_2$ branched dorsal-fin rays (vs. $9^1/_2$ in *M. bella* and *M. subhashi*, $9–10^1/_2$ in *M. maepaiensis*), and an air bladder with a free posterior chamber (vs. without in *M. subhashi*). It can be distinguished from *M. shanensis* by having $8^1/_2$ (vs. $9^1/_2$) branched dorsal-fin rays, a lower jaw without a median

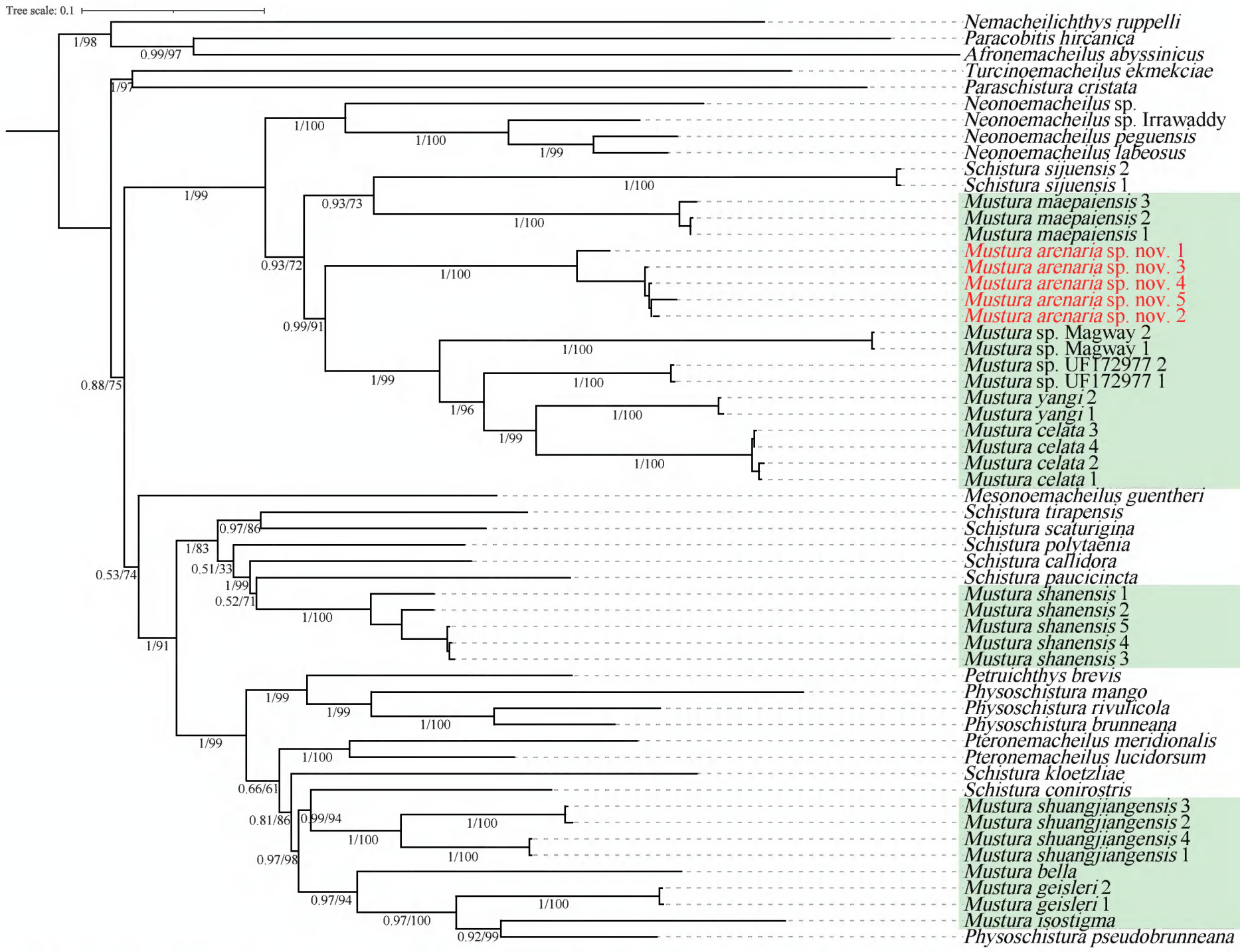

Figure 6. Bayesian phylogram of *Mustura* based on combined data of Cyt *b* and RAG1 sequences. Numbers on branches represent PP from BI and BS from ML. A green background indicates *Mustura* species.

Table 2. K2-P distance (%) between 11 species in the genus *Mustura* is based on the Cyt *b* gene.

Species	n	Intrasp. variation	Intersp. variation									
			1	2	3	4	5	6	7	8	9	10
1. *M. arenaria*	5	1.19										
2. *M. bella*	1	/	15.49									
3. *M. celata*	4	0.11	13.50	14.45								
4. *M. maepaiensis*	3	0.48	13.63	16.97	12.96							
5. *M. shanensis*	5	2.14	14.80	13.50	15.37	15.89						
6. *M. yangi*	2	0.09	14.35	16.25	10.19	13.04	15.31					
7. *Mustura* sp. Magway	2	0.00	14.99	18.45	14.01	16.21	17.45	12.80				
8. *Mustura* sp. UF172977	2	0.09	12.89	16.09	10.27	13.98	16.50	9.46	13.02			
9. *M. geisleri*	2	0.09	16.16	12.45	15.79	16.72	14.19	15.19	18.57	15.51		
10. *M. isostigma*	1	/	15.92	13.27	13.77	14.57	14.59	15.27	17.94	16.44	11.46	
11. *M. shuangjiangensis*	4	5.17	15.82	12.77	15.29	15.16	11.52	14.57	18.18	15.50	12.44	13.36

notch (vs. with a well-marked notch), and the presence (vs. absence) of a suborbital flap in males. It differs from *M. shuangjiangensis* by having 9–17 (vs. 6–10) dorsal saddles, a caudal peduncle depth of 8.7–10.5% SL (vs. 11–13% SL), and an air bladder with (vs. without) a free posterior chamber.

Mustura arenaria shares the presence of irregular, oval, or elongated lateral blotches alternating with dorsal saddles with other species in the complete lateral-line group. However, it can be distinguished from *M. celata* and *M. yangi* by having elongated to oval lateral blotches distinctly narrower than the interspace (vs. irregular blotches distinctly wider than the interspace), an upper lip with (vs. without) a median notch, and 8+8 caudal-fin rays (vs. 9+8 in *M. celata*). It differs from *M. harkishorei* by lacking (vs. possessing) a filamentous extension on the second branched pectoral-fin ray and 8+8 (vs. 7+8) caudal-fin rays. The new species is further distinguished from *M. isostigma*, *M. prashadi*, *M. taretensis*, and *M. tigrina* by having 8+8 (vs. 9+8, rarely 8+8 or 8+7 in *M. taretensis*) caudal-fin rays, $8^{1}/_{2}$ branched dorsal-fin rays (vs. $9^{1}/_{2}$ in *M. prashadi* and *M. tigrina*,

Table 3. Morphological comparison among species of *Mustura*. BDR = branched dorsal-fin rays, BCR = branched caudal-fin rays, MUP = marked on upper lip, MLJ = marked on lower jaw, BPR = branched pectoral-fin rays, FPA = free posterior chamber of the air bladder.

Taxon	River basin	BDR	BCR	Lateral bars/blotches and saddles on back	Basicaudal pattern	MUP	MLJ	BPR 2nd	Suborbital falp	FPA
Incomplete lateral-line group										
M. chhimtuipuiensis	Kaladan	8½	8+7	11–14 bars, continuous	2 blotches	present	absent	not modified	present	present
M. dikrongensis	Brahmaputra	8½	8+7	11–15 blotches, alternate or continuous	complete	present	absent	not modified	present	present
M. walongensis	Brahmaputra	8½	9+8	11–18 bars, continuous	w-shaped	present	absent	not modified	present	unknow
M. chulabhornae	Chao Phraya	8½	8–9+8	8–10 blotches alternate with 8–10 saddles	spot + blotch	present	absent	not modified	present	present
M. geisleri	Chao Phraya	8½	9+8	5–8 blotches alternate with 6–8 saddles	spot + blotch	present	absent	not modified	present	unknow
complete lateral-line group										
M. arenaria	Irrawaddy	8½	8+8	7–15 blotches alternate with 9–17 saddles	spot + blotch	present	absent	not modified	present	present
M. bella	Mekong	9½	9+8	12–30 blotches, continuous, 1 stripe	spot + blotch	present	absent	not modified	present	unknow
M. celata	Irrawaddy	8½	9+8	6–10 blotches alternate with saddles	spot + blotch	absent	absent	not modified	present	present
M. chindwinensis	Irrawaddy	8½	8+8	13–17 bars alternate with 11–16 saddles	spot + blotch	absent	present	not modified	present	present
M. daral	Brahmaputra	8½	9+8	9–10 bars, continuous	short blotch	present	absent	not modified	present	unknow
M. harkishorei	Brahmaputra	8½	7+8	8–10 blotches alternate with 8–10 saddles	2 blotches	unknow	absent	filamentous, extended	present	present
M. maepaiensis	Salween	9–10½	9+8	10–13 bars, continuous	spot + blotch	absent	absent	not modified	present	unknow
M. prashadi	Irrawaddy	9½	9+8	9–12 blotches alternate with saddles	2 blotches	present	absent	not modified	present	present
M. shanensis	Salween	9½	8+8	7–10 blotches, usually continuous	spot + blotch	present	present	not modified	absent	present
M. shuensis	Irrawaddy	9½	9+8	6–9 bars, continuous, a faint stripe	2 blotches	present	present	not modified	present	unknow
M. subhashi	Brahmaputra	8½	9+7–8	14–23 bars, continuous	short blotch	present	small/ absent	not modified	present	absent
M. taretensis	Irrawaddy	9–10½	8–9+7–8	12–13 blotches alternate with 11–16 saddles	2 blotches	present	absent	not modified	present	present
M. tigrina	Irrawaddy	9½	9+8	12–14 blotches alternate with 5–6 saddles	complete	present	absent	not modified	present	present
M. tuivaiensis	Brahmaputra	8½	8+7	12–14 blotches alternate with 15–17 saddles	2 blotches	present	present	not modified	present	present
M. yangi	Irrawaddy	8–9½	8+8	6–7 blotches alternate with saddles	spot + blotch	absent	small/ absent	mot modified	present	present
M. yunnaniloides	Irrawaddy	8½	8+8	18–20 blotches alternate with 14–16 saddles	spot + blotch	unknow	absent	not modified	present	absent
M. isostigma	Mekong	8½	9+8	5–7 blotches alternate with 5–7 saddles	2 spots	present	absent	not modified	present	unknow
M. shuangjiangensis	Mekong	8½	8–9+8	10–21 blotches, some connected with 6–10 saddes	1 bar	unknow	absent	not modified	present	absent

9–10½ in *M. taretensis*), 7–15 lateral blotches (vs. 5–7 in *M. isostigma*), a caudal fin without pigment (vs. with V-shaped markings in *M. prashadi*, *M. taretensis*, and *M. tigrina*), a basal caudal bar dissociated into an upper spot and a lower blotch (vs. complete in *M. tigrina*), and a forked caudal fin (vs. slightly forked in *M. prashadi*). *Mustura arenaria* differs from *M. tuivaiensis* by having 8+8 (vs. 8+7) caudal-fin rays, a caudal fin without pigment (vs. two rows of spots), and a lower jaw without (vs. with) a median notch. It differs from *M. yunnaniloides* by having a free posterior chamber of the air bladder (vs. absent) and 7–15 (vs. 18–20) elongated blotches. Finally, *M. arenaria* can be distinguished from its most similar species, *M. chindwinensis*, by having 7–15 blotches distinctly narrower than the interspace (vs. 13–17 blotches equal to or wider than the interspace), an upper lip with (vs. without) a median notch, a lower jaw without (vs. with) a median notch, and six (vs. seven) preoperculo-mandibular pores.

Discussion

Mustura arenaria sp. nov. is a member of *Mustura* because it shares the diagnostic characters of the genus as defined by Kottelat (2018). The validity of the new species is supported by its monophyly in the phylogenetic analysis (Fig. 6) and by the genetic distance divergence from other congeners (Table 2).

Most species currently assigned to *Mustura* were previously classified in *Physoschistura* or *Schistura*, and the taxonomic status of several species remained provisional pending further revision (Kottelat 2018). However, the reclassification proposed by Kottelat (2018) lacked strong genetic support. Recent phylogenetic studies of nemacheilid loaches have consistently demonstrated that *Mustura* does not form a monophyletic group (Dvořák et al. 2022, 2023; Šlechtová et al. 2025). Our results, based on an analysis of 11 species of *Mustura*, support this conclusion (Fig. 6). Specifically, the type species *M. celata*,

together with *M. maepaiensis*, *M. arenaria*, *M. yangi*, two uncertain taxa (*Mustura* sp. Magway and *Mustura* sp. UF172977), and *S. sijuensis*, form a well-supported clade (PP = 0.93, BS = 72), which is the sister group to the genus *Neonoemacheilus*. The remaining species are grouped within *Schistura*, *Physoschistura*, and other genera. Although true *Mustura* species share morphological features, such as mouth structure and sexual dimorphism, with *Pteronemacheilus*, *Physoschistura*, and *Petruichthys*, molecular evidence indicates clear genetic divergence among these groups. This pattern suggests that *Mustura* and related genera may have undergone morphological convergence during adaptive evolution, resulting in unclear genus-level diagnostic characters.

Mustura shanensis (originally described as *Nemacheilus shanensis*) has a complex and contentious taxonomic history. Kottelat (1990) initially placed this species in *Physoschistura* and noted that the structure of the air bladder could not be examined. Kottelat (2018) subsequently transferred it to *Mustura* based on color pattern and caudal-fin morphology. Bănărescu and Nalbant (1995) regarded its generic affiliation as uncertain and tentatively assigned it to the *Schistura rupecula* group. Our examination of *M. shanensis* specimens from Inle Lake reveals that this species shares several characters with *Schistura* while differing notably from both *Mustura* and *Physoschistura*: (1) absence of sexual dimorphism; (2) an anterior chamber of the air bladder divided into separate halves connected by a manubrium, with a distinct oval posterior chamber; and (3) a lower lip that is broadly interrupted, lacking the triangular cushion-like pads typical of *Mustura* (Fig. 7). Our phylogenetic analyses strongly support *M. shanensis* as an independent lineage sister to *Schistura* species (PP = 1, BS = 100), consistent with recent studies (Dvořák et al. 2022, 2023; Šlechtová et al. 2025). Therefore, based on both morphological and molecular evidence, we propose the reassignment of *M. shanensis* to the genus *Schistura* rather than *Mustura* or *Physoschistura*.

Genetic evidence further indicates that *M. bella*, *M. isostigma*, and *M. shuangjiangensis* (from the Mekong River drainage), together with *M. geisleri* (from the Chao Phraya River drainage), are more closely related to *Physoschistura* and *Schistura* than to true *Mustura* species (Fig. 6). Kottelat (2018) noted that the placement of these species in *Mustura* is provisional because several of their diagnostic characters deviate from those of typical congeners. *Mustura shuangjiangensis*, in particular, was considered morphologically distinct enough to represent a new genus, a view that conflicts with molecular evidence (Kottelat 2018; Endruweit 2025; Šlechtová et al. 2025). *Mustura daral*, *M. dikrongensis*, *M. harkishorei*, *M. subhashi*, and *M. walongensis* are distributed in the upper Brahmaputra River drainage in Arunachal Pradesh, which is geographically isolated from the Irrawaddy River basin (Fig. 5). A weaker affinity with *Mustura* is indicated by their more elongated body form and color pattern (Kottelat 2018). Furthermore, *M. harkishorei* has been regarded as a synonym of "*Nemacheilus corica*" due to overlapping distribution areas and similar morphological traits (Choudhury et al. 2021). As a result, relying exclusively on external morphological characters to definitively establish the taxonomic status of newly described

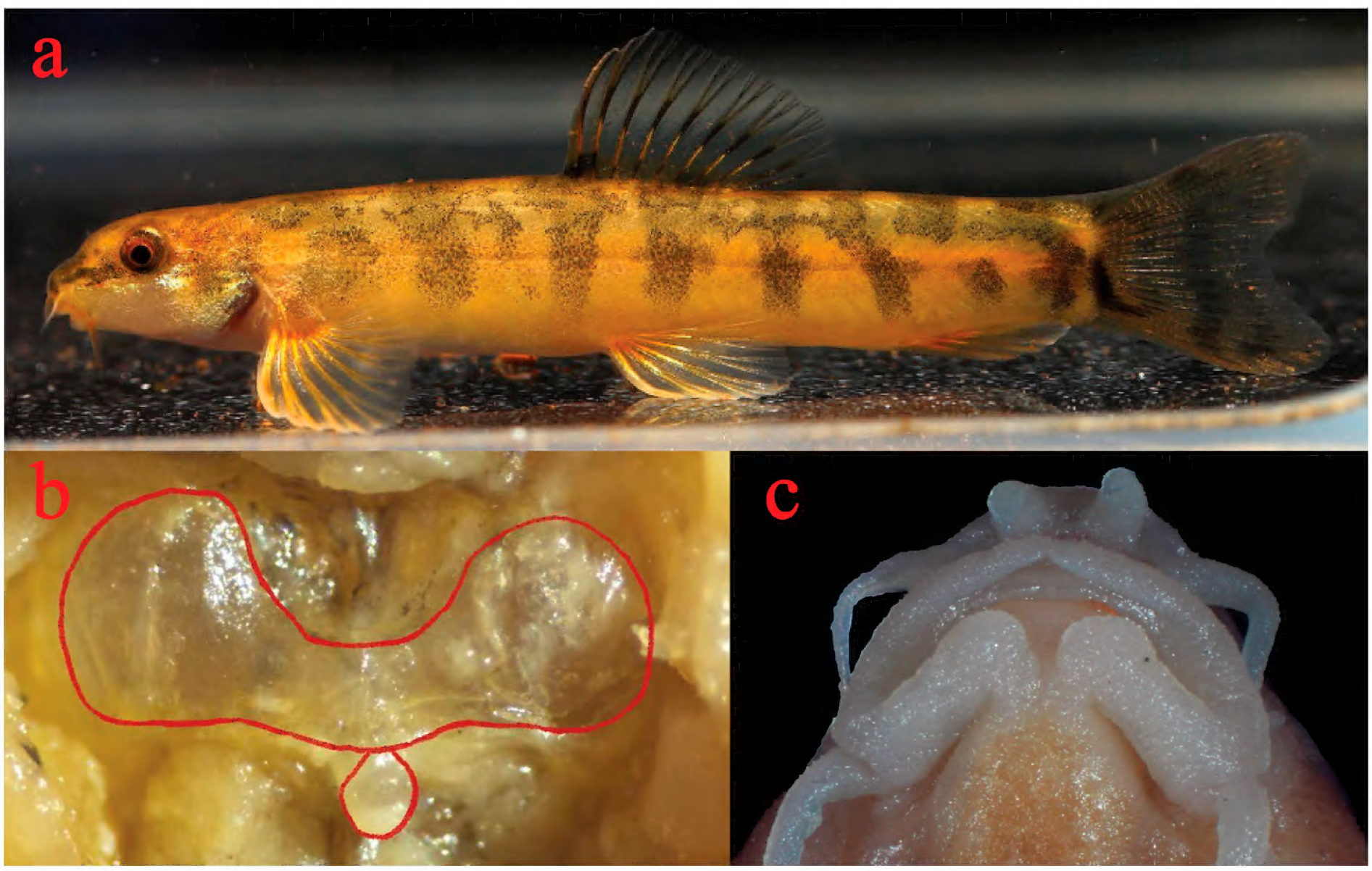

Figure 7. *Schistura shanensis*, Myanmar: Shan State: Yae Pale Stream, a tributary of Inle Lake. **a.** Lateral view of SEABRI 20182081, 36.6 mm SL (from Qin et al. 2022); **b.** Air bladder of SEABRI 20182081; **c.** Mouth structure of SEABRI 20182082, 36.5 mm SL.

species and their assigned taxa remains challenging. Therefore, further verification using integrative taxonomic approaches is necessary. In particular, additional studies incorporating systematic morphological comparisons and molecular analyses with broader species coverage are required to clarify which genera these species belong to or whether they represent distinct new genera.

Mustura currently lacks unique diagnostic characters that allow it to be effectively distinguished from related taxa, as evidenced by discrepancies between morphology and genetics. Regarding air bladder structure and variation in male pectoral fins, Zhu (1986) noted that morphological variation in the air bladder is associated with water velocity, implying limited taxonomic significance at the generic level. Moreover, Kottelat (2018) pointed out that variation in preservation methods and anatomical techniques may make it difficult to identify the posterior chamber of the air bladder. Although Zhu (1989) noted that rigid and broadened male pectoral-fin rays represent sexually dimorphic traits in Nemacheilidae, our findings show that this phenomenon occurs only probabilistically. In conclusion, while variation in male pectoral-fin morphology and air bladder structure, especially the posterior chamber, may be significant for species-level classification, these characters must be applied cautiously at the generic level. Collectively, these results suggest that, due to extensive overlap in diagnostic characters and inconsistencies between genetic and morphological data, the current generic classification of nemacheilid loaches in South and Southeast Asia requires comprehensive revision, particularly for *Schistura* and related genera.

Comparative material

Mustura celata: SEABRI 20182719–36, 18 ex., 14.8–35.9 mm SL, Myanmar: Kachin State: Indawgyi Lake basin: Mote Soe stream; SEABRI-CXY20190744, 3 ex., 23.5–39.5 mm SL, Myanmar: Kachin State: Indawgyi Lake basin: Nan Sa Pe Stream.

Mustura shanensis: SEABRI 20182081–2093, 13 ex., 20.9–47.6 mm SL, Myanmar: Shan State: Inle Lake basin: Yae Pale stream.

Mustura yangi: SEABRI 20160149–150, 347–353, 9 ex., 41.0–56.0 mm SL, Myanmar: Kachin State: Putao fish market.

Mustura shuangjiangensis: KIZ810443, KIZ810417–810426, KIZ81042–810437, KIZ810439–810441, KIZ 810444, 21 ex., 39.0–55.0 mm SL, China: Yunnan Province: Shuangjiang County: Xiaohei River.

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Supplementary material 1

Additional information

Authors: Jian-Bing Lyu, Feng Lin, Thaung Naing Oo, Xiao-Yong Chen

Data type: docx

Explanation note: **table S1.** Voucher and GeneBank accession number of Cyt *b* and RAG1 sequence. **table S2.** Sequence information and results of model selection by ModelFinder and PartitionFinder. **fig. S1.** 50% major-rule consensus of the Bayesian tree based on Cyt *b*. **fig. S2.** 50% major-rule consensus of the Bayesian tree based on RAG 1.

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